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Cuphea growth, yield, and oil characteristics as influenced by climate and soil environments across the upper Midwest USA☆

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ABSTRACT

Cuphea is a potential new oilseed crop rich in medium-chain fatty acids (C8:0 to C14:0) that may serve as a renewable, biodegradable source of oil for lubricants, motor oil, and aircraft fuel. Impacts of climate and soil environment on cuphea growth and development are not well understood. The objective of this study was to evaluate the influence of climate and soil on growth, seed yield, and seed oil characteristics of two semi-domesticated cuphea genotypes [PSR23 and HC-10 (*Cuphea viscosissima* Jacq. × *C. lanceolata* W.T. Aiton)] and three wild species [*Cuphea wrightii*, *Cuphea lutea*, and *C. viscosissima* (VS-6-CPR-1)] that show potential for domestication. The study was conducted in 2007 and 2008 at field sites in North Dakota (ND), Minnesota (MN), Iowa (IA), and Illinois (IL). Cuphea PSR23 and HC-10 were direct seeded in the field, while the three wild species were transplanted. The two plantings were treated as separate experiments. Plant growth, seed yield and oil content for the two direct-seeded lines tended to be distinctly greater in MN and ND than IL and IA, which was related more to growth temperature than soil environment. The three wild species generally performed similarly across the four different environments. *C. wrightii* had the greatest oil content, ranging from 320 to 360 g kg^{-1}, which was comprised of 59–64% lauric acid. For each genotype, the content of its most prominent saturated medium-chain fatty acid (e.g., C10:0 or C12:0) increased with decreasing latitude of field site. Seed yields for *C. wrightii* and *C. lutea* were as high as 1116 kg ha^{-1}. Combined with relatively high seed oil contents (280–350 g kg^{-1}) these species may be good candidates for domestication. Results indicate that PSR23 and HC-10 are more regionally adapted than the wild species studied, which tended to exhibit a greater range of adaptability to climate and soil conditions.

1. Introduction

Medium-chain fatty acids (MCFAs) derived from plant oils are highly desired for industrial chemical manufacturing of a wide range of products including soaps and detergents, lubricants, and personal care products (Thompson, 1984; Arkcoll, 1988). In the USA and many other developed countries, the primary source of plant-derived MCFAs are coconut (*Cocos nucifera* L.) and palm kernel (*Elaeis guineensis* Jacq.) oils. Recently, however, cuphea (cultivar PSR23) another rich source of MCFA, has been produced agronomically in the upper Midwest USA on a small scale (Gesch et al., 2006), and its seed oil has been targeted for cosmetic and personal care product manufacturing (Brown et al., 2007). The genotype PSR23 (Knapp and Crane, 2000) is the most agronomically promising, despite challenges such as seed shattering and indeterminacy (Gesch et al., 2006).

In addition to well established uses, MCFA derived from plants may be well suited for several new uses and processes being developed in the area of liquid biofuels, lubricants, and polymers. For instance, cuphea-oleic estolides synthesized from PSR23 cuphea oil make an exceptional engine lubricant with good low temperature properties (Cermak and Isbell, 2004). Also, Geller et al. (1999) have shown that cuphea oil rich in caprylic (C8:0) and capric acids (C10:0) has fuel properties similar to No. 2 diesel without being converted to the methyl ester. Moreover, because the fatty acid (FA)

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chain lengths of cuphea are naturally similar in length to that of the hydrocarbon chains in jet fuels, it may lend itself well to an energy and economically efficient process of manufacturing military jet fuel (personal communication; C. Wocken, Energy & Environmental Research Center, Grand Forks, ND).

Within the genus *Cuphea* there are 260 or more species most of which tend to emphasize the synthesis and storage of a particular MCFA (Graham et al., 1981). PSR23 cuphea primarily produces capric acid, which tends to comprise about 70–75% of its total seed oil (Knapp and Crane, 2000; Forcella et al., 2005). However, also having agronomically compatible cuphea genotypes rich in caprylic, lauric (C12:0), and myristic acids (C14:0), or various proportions of these FAs in their seed oil, would be beneficial for meeting both established and newly developing MCFA uses. There are certain species of cuphea that are rich sources of lauric acid or with similar proportions of two or more MCFAs in their seed oil profile that may be worthy of domestication for agronomic purposes. Two such species are *Cuphea wrightii*, which is rich in lauric acid, and *Cuphea lutea*, which tends to have a blend of about 29, 38, and 12% capric, lauric, and myristic (C14:0) acids, respectively (Graham, 1989). Both of these species have been field-grown to maturity and studied in central California (Hirsinger, 1985) and west-central IL (Phippen et al., 2006). However, little is known with regards to how growth, seed yield, and seed characteristics are affected by climate and soil environments for these species.

Previously, Forcella et al. (2005) reported that seed yield and oil content of PSR23 cuphea tended to decline with decreasing latitude in the northern Corn Belt along a transect between southwestern IA to northwestern MN. These authors concluded that the trend in seed yield was partly related to growth temperature and also suggested soil environment may have played a significant role in influencing seed yield.

The objective of the present study was to primarily evaluate the influence of climate and soil environment on plant growth, yield, and seed oil characteristics of two semi-domesticated genotypes PSR23 and HC-10, and the three wild species *C. wrightii*, *C. lutea*, and a seed oil mutant of *Cuphea viscosissima*, VS-6-CPR-1 (Tagliani et al., 1995).

2. Materials and methods

2.1. Plant culture

Soil and climate environments were varied by conducting the study at four locations throughout the upper Midwest USA in 2007 and 2008. The locations were Macomb, IL (lat-long; 40°3′N, 90°4′W) on an Osco silt loam soil (fine-silty, mixed, superactive, mesic Typic Argiudolls); Ames, IA (42°2′N, 93°3′W) on a Clarion loam soil (fine-loamy, mixed, superactive, mesic Typic Hapludolls); Morris, MN (45°3′N, 95°5′W) on a Barnes loam soil (fine-loamy, mixed, superactive, frigid Calcic Hapludolls); and Prosper, ND (46°5′N, 97°1′W) on a Perella silty clay loam (fine-silty, mixed, superactive, Typic Endoaquolls).

Five cuphea genotypes were grown at each study location. These included PSR23, HC-10, *C. wrightii* (accession: Ames 17789), *C. lutea* (accession: Ames 22410), and VS-6-CPR-1 [here after referred to as VS-6 (accession: PI 574621; Tagliani et al., 1995)]. VS-6 has lower capric, but higher caprylic and myristic acid content than its wild-type relative, *C. viscosissima* (Knapp et al., 1997). Seeds of PSR23 and HC-10 cuphea were obtained from plants grown in west-central MN and seeds of the other three genotypes were obtained from the USDA-ARS-North Central Regional Plant Introduction Station in Ames, IA.

The experimental design at all sites was a randomized complete block replicated four times for each of the two planting methods, direct seeding and transplanting. Each plot was 2.2 m × 1.2 m consisting of four rows spaced 0.60 m apart. PSR23 and HC-10 were direct seeded at a 6.0 mm depth with a single-row planter (model 1001-B, Earthway Products, Inc., Bristol, IN) at a rate of 11.2 kg ha^{-1}. The seeder was calibrated with PSR23 seed before use in the field. Because of seed dormancy, *C. wrightii*, *C. lutea*, and VS-6 were pregerminated and started in a greenhouse before being transplanted in the field.

In brief, *wrightii* and *lutea* seeds were exposed to a temperature of 45 °C for 1 h according to Crane et al. (2003) before being placed on moist germination paper and germinated in an incubator at a 25/15 °C day/night temperature and 12 h photoperiod. Seeds of VS-6 were placed on moist germination paper and stored in the dark at 4 °C for 42 d before being transferred to an incubator to germinate under a 25/15 °C day/night temperature and 12 h photoperiod. Germinated seed was transferred to 72-well trays (one seedling per well); each well had a volume of 96 cm^3 and was filled with a commercial potting soil (Miracle-Gro Potting Mix, Scotts Miracle-Gro Company, Marysville, OH) and grown in a greenhouse in Morris, MN under day/night temperatures of 21/18 °C in 2007 and 25/17 °C in 2008. The seedlings were started in the greenhouse on 27 March in 2007 and 1 April in 2008, at least 4 wk prior to being transferred to the field, and seedlings were placed outside during daylight hours (between 0900 and 1700 h CST) for hardening 4–7 d prior to transferring to the field.

Seedlings were transplanted to the field at the same time that PSR23 and HC-10 were direct seeded. Transplanted seedlings were spaced approximately 50 mm apart within rows to give a plant population density of approximately 89,100 ha^{-1}. Because of limited seed supply in 2007, *C. wrightii*, *C. lutea*, and VS-6 were transplanted in two rows with an adjacent boarder row of soybean [*Glycine max* (L.) Merr.] on each side. Once established, the soybean was kept pruned to the same height as the cuphea throughout the season. This was done to reduce border effects and is a technique successfully used previously (Gesch et al., 2002). This was not necessary in 2008, and all plots consisted of four rows of transplants.

All plots were treated with trifluralin [2,6-dinitro-N,N-dipropyl-4-(trifluoromethyl)aniline] at 1.1 kg active ingredient ha^{-1}and broadcast with N, P, K, and S at 90, 34, 45, and 34 kg ha^{-1} and both herbicide and fertilizer were incorporated into the soil at least 48-h before planting. The planting dates in 2007 and 2008 were 7 May and 5 May in IL, 14 May and 13 May in IA, 15 May and 20 May in MN, and 16 May and 21 May in ND, respectively. Irrigation was applied at the MN site because this location experienced severe drought and plants showed symptoms of drought stress. Only enough water was applied to achieve what plants would normally experience during an average (i.e., rainfall) year. Irrigated water applied was 35, 28, and 32 mm on 6 July, 24 July, and 9 August in 2007, respectively, and 44 mm on 30 July in 2008. The other sites did not require irrigation due to normal to above normal rainfall patterns. Air temperature and rainfall were continuously collected throughout the growing season at automated weather stations located on-site at the IA, MN, and ND study sites and located at an airport within 6 km of the IL site. Air temperature data, including that from the greenhouse for the transplanted species, was used to calculate growing degree days (GDD; °C d) using a base temperature (T_{base}) of 10 °C for all genotypes from planting to harvest. Growing degree days were calculated as: $\mathrm{GDD} = \sum(T_{max} + T_{min}/2) - T_{base}$, where T_{max} and T_{min} are daily maximum and minimum air temperature, respectively.

2.2. Soil and plant sampling

Soil bulk densities were measured before planting and after harvest in 2007 and 2008 by collecting two cores from each experimental block with a 51-mm diameter probe and separating them into 0–0.15- and 0.15–0.30-m depth segments. Each segment was oven dried (105 °C) and weighed. Soil cores taken for bulk den-

sity were also used for determining water retention characteristics using the pressure plate method of Klute (1986).

Soil moisture at the 100-mm depth was measured continuously throughout the growing season with EC-5 moisture sensors (Decagon Devices, Inc., Pullman, WA) buried in three of the four replicated blocks at each site. The sensors were interfaced to data loggers (HOBO Micro Station, Onset Computer Corporation, Pocasset, MA) that recorded measurements every 30 min. The data shown represent daily averages.

Plant height was measured throughout the season at 3–4-wk intervals. All cuphea genotypes were harvested in early to late September corresponding to approximately 1200–1400 °C d GDD. Criteria of when to harvest was based on previous results for cuphea PSR23 (Gesch et al., 2005; Berti and Johnson, 2008). Plants were hand harvested from the middle two rows (1.44 m^2) and dried in a forced air oven at 65 °C for 48 h. After determining total biomass, plants were threshed and seed was cleaned by screening for determining yield.

Although PSR23 and HC-10 have improved seed retention, seed shattering is still an issue (Gesch et al., 2006), especially for the wild species studied (Graham, 1989). Therefore, for all plots at each site, a 0.51 m × 0.25 m × 0.06 m deep plastic container was buried in the soil between the two harvest rows to catch shattered seed. These "seed traps" contained holes in the bottom and were lined with fine mesh screen to allow water to escape. For PSR23 and HC-10, seed contained in the traps was collected at harvest, cleaned, and the mass per area determined. This was then added back to the final yield. Since the wild species have more extensive seed shatter, the seed was collected from the traps on a weekly basis up to harvest and then added to the final yield. This was done to give a better estimation of potential yield at each site. All seed yields are reported on a 120 g kg^{-1} seed-moisture basis. Harvest index (HI) was calculated as total dry seed mass divided by total dry biomass.

Seed oil content was measured by pulsed nuclear magnetic resonance (Bruker Minispec pc120, Bruker, The Woodlands, TX) as previously described by Gesch et al. (2005). Moisture content analysis was conducted according to AOCS Method 2-75. Each sample was done in duplicate, dried at 130 °C for 3 h, and cooled in a desiccator for 15 min.

Fatty acid profiles of seed oil were measured by gas chromatography (Hewlett-Packard 5890 Series II, Palo Alto, CA) equipped with a flame-ionization detector and an auto-sampler/injector. Analyses were conducted on a SP-2380 30 m × 0.25 mm i.d. column (Supelco, St. Louis, MO) at a flow rate of 1.1 ml min^{-1} with helium head pressure of 25 psi; split ratio 50:1. Saturated C8–C30 fatty acid methyl esters (FAME) provided standards for making fatty acid and by-product assignments. The run temperatures were as follows: 120 °C for 3 min; ramp from 120 to 185 °C at 25 °C min^{-1} and hold for 4.4 min; ramp from 185 to 265 °C at 25 °C min^{-1} and hold for 0.4 min. Injector and detector temperatures were set at 250 °C. Approximately 25 mg of cuphea seed was grounded with a Modular Homogenizer System (Cole-Parmer Instrument Co., Vernon Hills, IL) placed in a vial and extracted with hexane. All samples were analyzed in triplicate.

The ANOVA procedure of SAS (SAS for Windows 9.1, SAS Inst., Cary, NC) was used to statistically compare mean differences in seed yield, biomass, and seed oil characteristics both within and across site locations. The semi-domesticated genotypes, which were direct seeded (i.e., PSR23 and HC-10), and the wild cuphea species, which were transplanted, were treated as two separate experiments. The method of Palmquist et al. (1993) was used to compare slopes of the linear relationship of plant height as a function of GDD for a given genotype among locations.

3. Results and discussion

3.1. Climate and soil characteristics

Average growing season temperatures were greater in 2007 than 2008 across all sites. The IL site was warmest, followed by IA, then MN, and ND (Table 1). In 2008, mean growing season temperature for IL was 4 °C cooler than in 2007 (Table 1). Growing degree days (°C d) are often used in association with crop growth and phenology to help predict plant growth stages (e.g., vegetative and reproductive growth phases). Berti and Johnson (2008) developed a descriptive model of growth stages for PSR23 cuphea from seedling emergence to harvest maturity based on GDD. For instance, they reported initial flowering (designated R1) occurring at 800–1000 GDD and harvest maturity (R5) at 1000–1250 GDD, using a base and upper-limit temperature of 10 and 30 °C, respectively. In west-central MN when cuphea was sown in early to mid-May, the optimum time to harvest was found to be between late September and early October (Gesch et al., 2005), which corresponded to about 1336–1354 GDD using a base of 10 °C, but no upper-limit temperature. In the present study, accumulated GDD from planting to harvest ranged from 1561 at the most southerly site (IL) to 1114 at the most northerly site (ND) in 2007 and ranged from 1418 at IL to 1057 at ND in 2008 (Table 1). Based on GDD, harvest timing was different at each research site due to the temperature difference.

From planting to harvest, in both years of the study, the IA field site received the most rainfall (Table 1). In 2008, especially from

Table 1
Monthly average air temperature, growing degree days (GDD; using a base temperature of 10 °C) and rainfall from planting to harvest at the four study sites.

Year	Date	Temperature (°C)				GDD (°C d)				Rainfall (mm)			
		IL	IA	MN	ND	IL	IA	MN	ND	IL	IA	MN	ND
2007	May[a]	21.0	18.3	16.3	15.2	181	152	116	84	38	100	47	43
	June	23.9	21.7	20.7	20.5	380	351	321	316	157	46	84	106
	July	25.1	23.6	22.4	22.1	437	420	384	376	50	67	10	49
	August	27.8	23.7	19.7	18.2	496	424	290	263	116	185	58	51
	September	25.9	18.9	16.5	14.9	68	63	104	76	0	0	22	36
	Mean	24.7	21.2	19.1	18.2	312	282	243	223	72	80	45	57
	Total	123.7	106.2	95.6	90.9	1561	1410	1214	1114	361	398	221	285
2008	May	15.6	15.7	14.9	14.7	152	108	59	53	54	118	18	31
	June	22.7	21.0	18.1	17.2	369	329	243	215	103	238	97	164
	July	24.1	23.1	21.7	20.5	436	406	363	325	68	201	31	75
	August	22.3	21.3	20.6	20.3	382	350	327	319	54	23	58	77
	September	18.7	15.9	15.8	14.9	78	59	174	144	43	7	61	180
	Mean	20.7	19.4	18.2	17.5	283	250	233	211	64	117	53	105
	Total	103.5	96.9	91.1	87.6	1418	1252	1166	1057	322	587	265	527

[a] Temperature and rainfall data collection began at the time of planting and ended at harvest.

Table 2
Soil bulk density at the 0–0.15 and 0.15–0.30 m depth for the four study sites in 2007 and 2008.

Year		IL (g cm^{-3})		IA (g cm^{-3})		MN (g cm^{-3})		ND (g cm^{-3})	
		0–0.15 m	0.15–0.30 m	0–0.15 m	0.15–0.30 m	0–0.15 m	0.15–0.30 m	0–0.15 m	0.15–0.30 m
2007	Spring	1.46 ± 0.03[a]	1.42 ± 0.05	1.48 ± 0.11	1.59 ± 0.02	1.16 ± 0.11	1.25 ± 0.07	1.29 ± 0.09	1.34 ± 0.05
	Fall	1.13 ± 0.03	1.43 ± 0.09	1.34 ± 0.14	1.53 ± 0.11	1.02 ± 0.03	1.02 ± 0.06	0.95 ± 0.05	1.19 ± 0.09
2008	Spring	1.22 ± 0.04	1.39 ± 0.09	1.40 ± 0.11	1.43 ± 0.14	1.07 ± 0.04	1.16 ± 0.11	1.27 ± 0.07	1.34 ± 0.03
	Fall	1.40 ± 0.03	1.48 ± 0.05	1.37 ± 0.11	1.60 ± 0.14	1.14 ± 0.08	1.25 ± 0.08	1.15 ± 0.06	1.30 ± 0.04

[a] Values are means ± SD, n = 4–6.

May through July, the IA site was extremely wet with standing water in plots for extended periods. The ND site was also unusually wet during the 2008 growing season. The driest site was in MN, which only received 221 mm of precipitation during 2007, an unusually dry summer, and plants were given supplemental irrigation primarily during July due to the onset of drought stress symptoms (i.e., leaf rolling and wilting) in plants.

Sharratt and Gesch (2004) reported that cuphea's maximum rooting depth was about 0.5 m in a loamy soil with most of its root length density occurring within the top 0.3 m of the soil profile. Due to cuphea's shallow and small root system, soil bulk density may be an important factor effecting its growth and yield. For instance, a low soil bulk density may allow roots to penetrate deeper to access additional nutrients and water in the soil. Generally, soil bulk densities were greater at the IL and IA sites than at the MN and ND sites with MN being the lowest (Table 2). For example, spring bulk densities at the 0.15–0.3 m depth at IA were 27 and 23% greater and fall measurements were 50 and 28% greater than at MN during 2007 and 2008, respectively (Table 2).

Soil water content was continuously monitored at a depth on 0.10 m throughout the growing season in 2007 and 2008 (Fig. 1). During both years of the study, soil water content was greatest at the IA site and remained so throughout the season, which was due to exceptionally high rainfall (Table 1). Also due to high precipitation, soil moisture at 0.1 m remained high throughout the season at ND in 2008. Generally, soil moisture was lowest at the IL site.

Plant available water (PAW) is the soil water content available for plant growth. Generally, it is accepted that PAW is the amount of stored soil water between field capacity (FC; water content at −0.03 MPa matric potential) and the permanent wilting point (PWP; water content at −1.5 MPa) of the soil, which varies with its physical structure (Kramer, 1983). Fig. 2 shows the relationship between gravimetric water content and soil matric potential (i.e., water retention curve) for each of the soils from the four study sites. All four soils were loams, and as might be expected, the degree of variation in water retention among them was not great. Soil water content between FC and PWP, or PAW, was greatest for the IL soil (105 g kg^{-1}), followed by ND (98 g kg^{-1}), then MN (93 g kg^{-1}), and was least for the IA soil (66 g kg^{-1}) (Fig. 2). Typically, yield for most crops is not compromised by maintaining soil water content at or near FC in the rooting zone (Taylor and Ashcroft, 1972), including PSR23 cuphea (Gesch et al., 2009). However, for most plants, exposure of roots to saturated or flooded soil for extended periods can be detrimental.

During both years in IA, soil water content at 0.1 m was near saturation for most of the growing season (Fig. 1). Some plants at the IA site, especially between June and July of 2008, suffered severe stress resulting from too much soil moisture (field observation). Soil water content tended to be lowest at the IL site followed by MN in both 2007 and 2008. These sites had relatively high soil water content early in the growing season (i.e., May through June), but became much drier throughout mid and late summer (Fig. 1). Crops can experience drought stress when soil water content falls below FC, especially when it reaches 50% PAW capacity or less (Kramer, 1983). By July of both years, the soil water content at the IL site declined greatly and was relatively low throughout much of the remainder of the growing season, which when combined with high air temperatures during July and August (Table 1), likely led to some degree of drought stress. In 2007, soil water content was initially high at the ND site, but consistently declined from late June to late August and might have caused plants to experience drought stress at this time. Care must be exercised in evaluating the data in Fig. 1 as it only represents a small portion of the soil profile, but nevertheless provides a means to compare soil moisture conditions throughout the season across locations.

For most crops, high temperature and drought stress experienced at the reproductive phase of development, can lead to substantial yield losses (Barnabás et al., 2008). Under controlled-environment conditions, Gesch and Forcella (2007) found that growth rate of reproductive tissues (i.e., flower capsules and seed) of PSR23 cuphea linearly declined when daily mean air temperature was increased from 15 to 27 °C. They concluded that its seed production may be better suited for regions with relatively cool

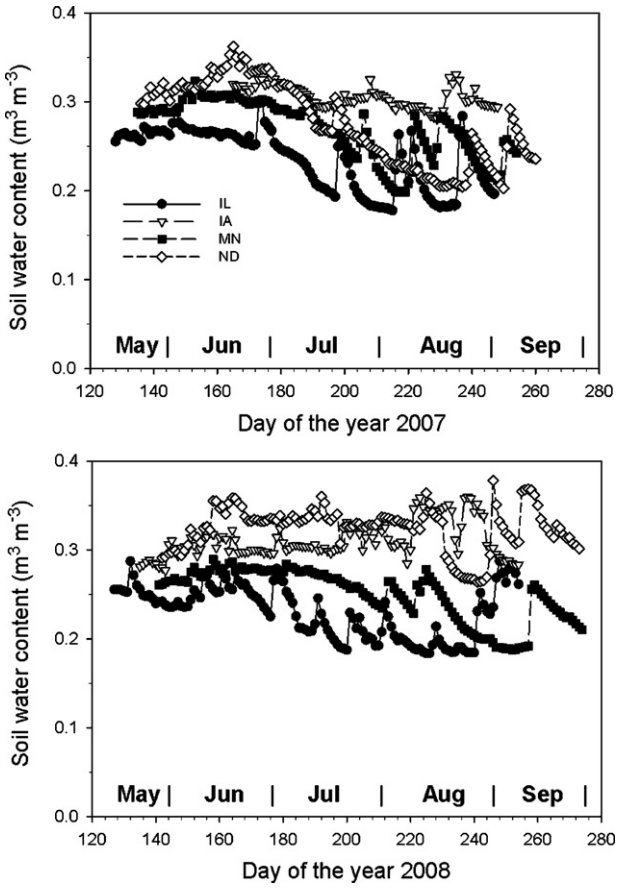

Fig. 1. Volumetric soil water content measured at 0.10-m below the soil surface. Values are daily means, n = 3. *Experimental sites*: Illinois (IL), Iowa (IA), Minnesota (MN), and North Dakota (ND).

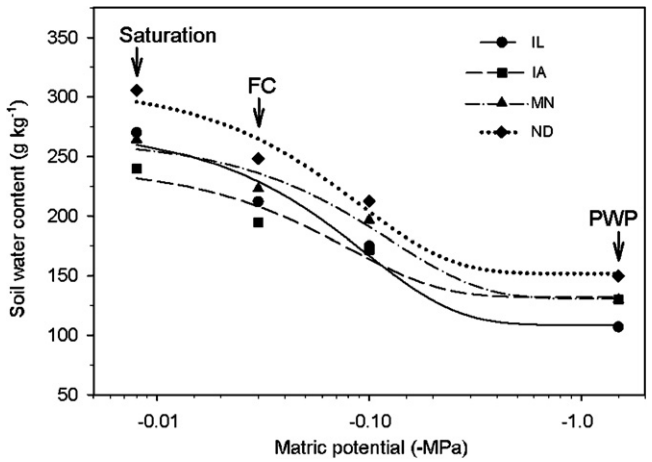

Fig. 2. Gravimetric soil water retention curves for the 0- to 0.15-m depth of soil from each of the four study sites. Values are means based on measurements of duplicate intact soil cores from each site. Arrows denote points of saturation, field capacity (FC), and permanent wilting point (PWP). *Experimental sites*: Illinois (IL), Iowa (IA), Minnesota (MN), and North Dakota (ND).

to moderate air temperatures. PSR23 and HC-10 cuphea grown in the upper Midwest, when sown in May, begin reproductive phase in mid to late July (Berti and Johnson, 2008; Gesch et al., 2002) and because of indeterminacy, continue to flower until killed by frost. Therefore, at least for these genotypes, the months of July and August can be quite critical for good seed set and production. This also tends to be the time when they are most prone to high temperatures and drought in the upper Midwest.

Less is known about the timing of flowering and seed production for the three wild species used in our study. In a study conducted by Hirsinger (1985) at Davis, California, which exhibits a Mediterranean-type climate, the time of flowering for *C. wrightii* and *C. viscosissima* was found to be about 60–65 d after planting and for *C. lutea* was less than 50 d. In Hirsinger's experiment, seedlings of these species were also started in a greenhouse from pre-germinated seed and transferred to the field. However, no temperature or GDD information was given for the study. Moscheni et al. (1994) report, that for *C. lutea* seedlings started in a greenhouse and transplanted in early May in Pisa, Italy the days from planting to flowering were 40–42 d. In our study, the timing of flowering in the field for the wild species may have been confounded somewhat because of starting seedlings in a greenhouse before transplanting, although accumulated GDD were recorded for these plants prior to transplanting. Both *C. wrightii* and *C. lutea* began flowering before VS-6 in the field, but all three tended to begin flowering before the direct-seeded genotypes, PSR23 and HC-10. With respect to days from planting to initial flowering in 2007 across all sites, *C. wrightii* ranged from 45 to 51 d, *C. lutea* from 55 to 56 d, and VS-6 from 54 to 61 d, while that for PSR23 and HC-10 ranged from 61 to 66 d.

3.2. Plant growth and yield

Plant height was used as a means of comparing growth rates of plants across experimental locations (Fig. 3). Measurements were taken throughout the season, plotted as a function of GDD, and analyzed by linear regression to compare slopes of the response (Table 3), which give the rate of plant height increase (cm GDD^{-1}). For PSR23 and HC-10, there was a trend for the slope of the response to increase with increasing latitude (i.e., from IL to ND; Table 3 and Fig. 3, PSR23). For a given genotype, linear response functions for height differed between locations based on comparison of full and reduced model *F*-tests (Table 3). In some instances the intercept of the equation rather than slope differed. For VS-6, *C. wrightii*, and *C. lutea* no clear trends developed across locations, although the rate of plant height increase was generally greatest for these species at

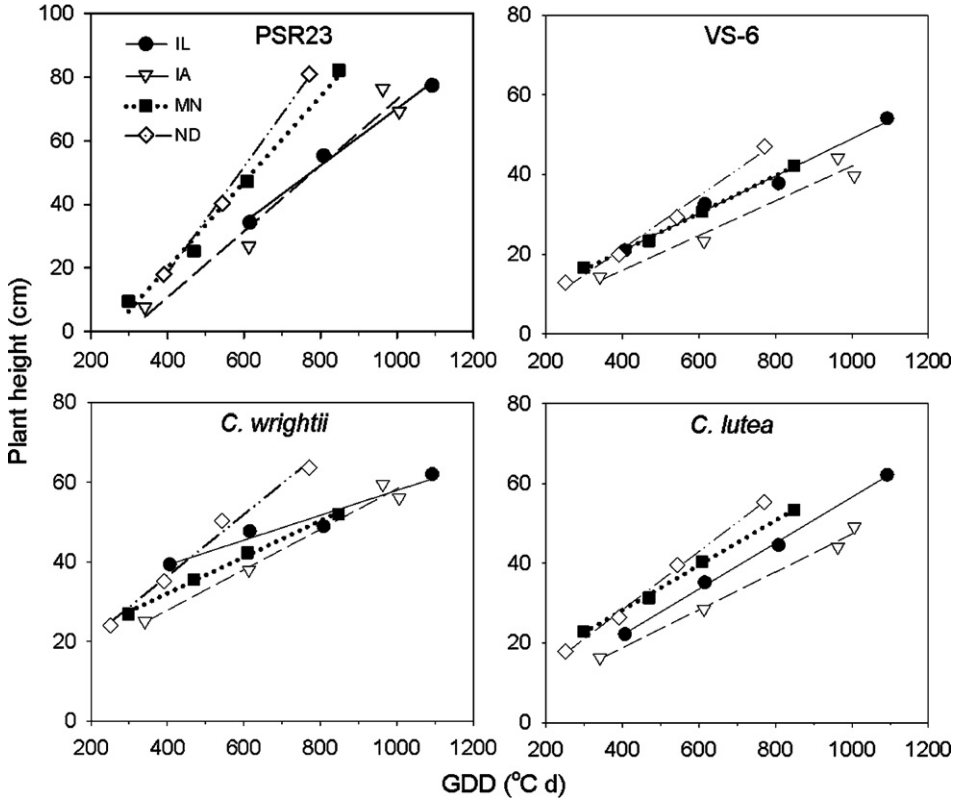

Fig. 3. Plant height as a function of growing degree days (GDD) in 2008. Values are means, $n = 4$; each replication was the mean of five different plants. HC-10 was very similar to PSR23 and therefore, not shown. *Experimental sites*: Illinois (IL), Iowa (IA), Minnesota (MN), and North Dakota (ND).

Table 3
Slopes and adjusted r^2 values for the linear regression analysis of plant height for the five cuphea genotypes studied.

Year	Location	PSR23		HC-10		VS-6		*C. wrightii*		*C. lutea*	
		Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2
2007	IL	0.065 b[†]	0.94[‡**]	0.065 a	0.87**	0.035 b	0.89**	0.040 ab	0.97**	–	–
	IA	0.066 b	0.90	0.064 a	0.88	0.037 b	0.99	0.020 b	0.87	0.030 a	0.99**
	MN	0.086 a	0.91	0.073 a	0.77	0.048 a	0.99	0.051 a	0.95	0.021 b	0.97
	ND	0.095 a	0.99	0.073 a	0.82	0.049 a	0.97	0.039 ab	0.74	–	–
2008	IL	0.089 b	0.99*	0.083 b	0.99**	0.048 ab	0.99**	0.032 b	0.89**	0.058 ab	0.99**
	IA	0.107 b	0.96	0.106 b	0.99	0.042 b	0.93	0.050 ab	0.95	0.047 b	0.99
	MN	0.128 a	0.96	0.124 ab	0.95	0.046 ab	0.99	0.048 ab	0.99	0.056 ab	0.99
	ND	0.158 a	0.99	0.161 a	0.99	0.059 a	0.94	0.078 a	0.99	0.074 a	0.99

[†] For a given genotype and year, slopes followed by the same letter are not significantly different at the $P \leq 0.05$ level.
[‡] For a given genotype and year, ** and * denote significant differences between location equations at the $P \leq 0.01$ and ≤ 0.05 level, respectively. Comparison of equations was done using full and reduced model *F*-tests.

the ND site, except for *C. wrightii* in 2007 (Table 3). By final harvest, the height for each genotype was similar across locations (Fig. 3). PSR23 and HC-10 were tallest at around 80–85 cm, while that of the other three genotypes ranged from 40 to 60 cm. These data indicate that the growth rates of PSR23 and HC-10 may be more regionally adapted, favoring soil and climate conditions present at the more northerly latitudes, while growth of the three wild species may be more widely adapted across the Midwest. A higher growth rate, particularly early in the growing season, can lead to earlier canopy closure and thus, better competition against weeds for light, nutrients, and water.

Similar to plant growth, seed and biomass yield of PSR23 and HC-10 tended to be distinctly greater at the two northerly sites (MN and ND) as compared to the southerly sites (IL and IA) (Table 4). The exception was ND in 2008, where biomass for the two direct-seeded genotypes was greater than that in IL, but seed yields were not significantly different. The ND site was very wet during 2008 (Table 1 and Fig. 1) and cooler than 2007, which might be why seed yields were low in 2008 (Table 4). Conversely, seed yields of PSR23 and HC-10 in IL during 2008 were nearly twice as high as in 2007 with similar biomass yields (Table 4). This yield increase was associated with a large drop in growing season temperature, which in August and September was considerably lower than in 2007 (Table 1). Also, drought stress or a greater degree of stress resulting from a combination of low soil moisture and high evaporative demand may have caused lower yields in 2007 (Fig. 1 and Table 1). The lower HI in 2007 as compared to 2008 also indicates potential drought and/or heat stress (Gesch et al., 2009). The relatively low yields in both years at the IA site (Table 4) were likely a result of too much rainfall, especially during 2008 (Table 1), but might also be related to soil structure. The IA site had the greatest soil bulk density (Table 2), which could have restricted root growth. No clear location trend developed with respect to seed shattering (Table 4) and it is unclear why shattering was generally greater in 2008 than 2007. Forcella et al. (2005) suggested that part of the reason for the decline in yield with decreasing latitude that they observed for PSR23, might have been partly due to greater shattering caused by potentially accelerated plant development resulting from higher growth temperatures. However, data from our study does not support that suggestion.

Like seed yield, oil content of PSR23 and HC-10 was generally greater at the ND and MN sites compared to the IL and IA sites. These findings tend to agree with those of Forcella et al. (2005) who reported seed and oil increases for PSR23 with more northerly latitude when grown along a transect between southern IA and northern MN. They showed that this was most closely related to a decrease in growth temperature with increasing latitude. The same relationship held true in the present study (Table 1 and Table 4). Moreover, the substantial increase in seed and oil yield at IL during the 2008 season when the mean growing season temperature declined by 4 °C compared to 2007, further verifies this relationship. The hot, dry conditions at IL in 2007 and excessively wet conditions at IA in both years were likely yield-reducing factors.

For PSR23 and HC-10, highest seed and biomass yields were recorded at the MN site, despite abnormally dry conditions during both years of the study (Table 1; for June through August average rainfall at the MN site over the past 120 yrs is 270 mm). In Forcella et al.'s study (2005), PSR23 yields also tended to be greatest at the Morris, MN site, the same site used in the present study. Apart from soil and climate, another possible reason for higher yields at the MN site may be closely related to pollinating insect health and abundance, especially that of native bees. PSR23 (and HC-10 because of its close relationship) is known to rely strongly on cross pollination by insects for fertility and seed set (Knapp and Crane, 2000). The field site in MN was adjacent to a lake (i.e., within 50–100 m) surrounded by a riparian area and in close

Table 4
Seed and biomass yield, harvest index (HI), and seed oil content of direct-seeded cuphea genotypes.

Genotype	Location	2007					2008				
		Seed yield ($kg\,ha^{-1}$)	Biomass yield ($kg\,ha^{-1}$)	Seed shatter (%)	HI	Oil ($g\,kg^{-1}$)	Seed yield ($kg\,ha^{-1}$)	Biomass yield ($kg\,ha^{-1}$)	Seed shatter (%)	HI	Oil ($g\,kg^{-1}$)
PSR23	IL	360 c[a]	5758 bc	40 a	0.06 b	270 b	720 b	5946 b	36 c	0.12	310 a
	IA	283 c	4283 c	21 b	0.06 b	280 b	245 c	2784 c	68 a	0.11	270 b
	MN	1155 a	10,772 a	16 b	0.11 a	330 a	1011 a	9171 a	64 ab	0.11	330 a
	ND	772 b	7577 b	22 b	0.10 a	330 a	548 b	8794 a	44 bc	0.06	320 a
	P-value	*<0.0001*	*0.0003*	*0.0001*	*0.002*	*<0.0001*	*0.0001*	*0.0003*	*0.03*	*0.17*	*0.0005*
HC-10	IL	320 c	5627 c	37 a	0.05 b	250 b	626 b	6138 b	75	0.10	300 b
	IA	255 c	4969 c	18 ab	0.05 b	270 b	55 c	580 c	39	0.13	210 c
	MN	873 a	10,265 a	20 ab	0.08 a	330 a	1191 a	8564 a	67	0.14	330 a
	ND	609 b	7780 b	16 b	0.08 a	320 a	508 b	8775 a	51	0.06	310 ab
	P-value	*0.0005*	*0.0005*	*0.13*	*0.009*	*0.0001*	*<0.0001*	*<0.0001*	*0.20*	*0.46*	*<0.0001*

[a] Values are means $n = 4$. Within columns for a given genotype and year, values followed by the same letter are not significantly different.

Table 5
Seed and biomass yield, harvest index (HI), and seed oil content of transplanted cuphea genotypes.

Genotype	Location	2007				2008			
		Seed yield (kg ha^{-1})	Biomass yield (kg ha^{-1})	HI	Oil (g kg^{-1})	Seed yield (kg ha^{-1})	Biomass yield (kg ha^{-1})	HI	Oil (g kg^{-1})
VS-6	IL	179 a[†]	6520	0.01 c	210 a	290 b	8437 a	0.04 c	280 a
	IA	292 a	5095	0.06 a	260 a	45 c	1376 b	0.03 c	190 b
	MN	241 a	6536	0.04 b	260 a	838 a	7444 a	0.11 a	270 a
	ND	69 b	6221	0.03 b	240 a	734 a	7859 a	0.09 b	260 a
	P-value	*0.005*	*0.23*	*0.0002*	*0.14*	*<0.0001*	*<0.0001*	*<0.0001*	*0.0002*
C. wrightii	IL	31 b	1921 b	0.02 b	330 b	1027 a	9388 ab	0.11 a	350
	IA	292 a	6713 a	0.05 a	350 a	186 c	4190 c	0.04 c	360
	MN	351 a	7519 a	0.05 a	350 a	666 b	8435 b	0.08 b	320
	ND	345 a	7779 a	0.05 a	350 a	660 b	10,252 a	0.06 bc	350
	P-value	*<0.0001*	*0.002*	*0.007*	*0.02*	*<0.0001*	*<0.0001*	*0.0002*	*0.44*
C. lutea	IL	[‡]–	–	–	–	854 b	9316 a	0.09 ab	310
	IA	454	3069 b	0.15 a	280	145 c	1980 b	0.08 b	280
	MN	492	7254 a	0.07 b	290	1116 a	9448 a	0.12 a	280
	ND	–	–	–	–	922 b	9199 a	0.10 a	300
	P-value	*0.76*	*0.002*	*0.01*	*0.09*	*<0.0001*	*<0.0001*	*0.02*	*0.09*

[†] Values are means $n = 4$. Within columns for a given genotype and year, values followed by the same letter are not significantly different.
[‡] *Cuphea lutea* was not grown in IL or ND during 2007.

proximity (closest 100 m) to several patches of native prairie grass and forbs. Typically, this site has a large population and diversity of pollinating insects (field observation). In contrast, the ND site was surrounded by intensively managed agricultural land, while the IA and IL sites were surrounded by a mix of urban and agricultural areas. Morandin and Winston (2006) clearly showed that native bee populations (*Apis* spp.) increased in direct relation to the amount of native uncultivated land adjacent to cultivated canola (*Brassica napus* L.) production. Furthermore, increased bee numbers led to higher productivity and economic returns in canola, which like cuphea, benefits from bee pollination (Morandin and Winston, 2006).

Unlike the two semi-domesticated genotypes, VS-6, *C. wrightii*, and *C. lutea* did not show any clear regional trends with respect to seed and biomass yields and oil content (Table 5). This taken together with results of similar growth rates across locations (Table 3) appears to indicate that these genotypes may be more widely adapted to climate and soil conditions than PSR23 and HC-10. It is important to note that all three wild species are self pollinating (Hirsinger and Knowles, 1984). Oil content was greatest for *C. wrightii* at 360 g kg^{-1} and lowest in VS-6, which ranged from 190 to 280 g kg^{-1} (Table 5). The high oil content of *C. wrightii* combined with a relatively high seed and biomass yield potential, at least as shown in 2008, may make it a worthy candidate for domestication. *C. lutea* may also be a good candidate for domestication as it yielded well across locations (with the exception of IA in 2008) and had modestly good seed oil content (280–310 g kg^{-1}). In late July of 2007, the *C. wrightii* grown at IL was almost completely killed by an unidentified disease. Interestingly, it did not affect any other genotype at the site. During 2008, seed and biomass yields were extremely low for all three wild species at the IA site due to flooding (Table 5). Of the wild species, VS-6 yielded the lowest across all sites and both years. The relatively low oil yield of VS-6 might be linked to its seed oil mutation, as wild-type *C. viscosissima* has greater seed oil content in comparison (Tagliani et al., 1995).

3.3. Seed fatty acid oil profiles

Both PSR23 and HC-10 are high capric acid (C10:0) producing genotypes (Gesch et al., 2006). In the present study, capric levels ranged from 75 to 84% (Table 6). HC-10 was bred for higher capric content than PSR23 (personal communication, S.J. Knapp). However, the capric levels for HC-10 were no higher than those of PSR23 (Table 6). PSR23 capric levels for our study are relatively high compared to those reported by others (Knapp and Crane, 2000; Forcella et al., 2005). Capric levels for both genotypes tended to be greatest in IL, which was the warmest site both years. For most oilseed crops, FA saturation often increases with increasing growth temperature, while unsaturation decreases (Tremollieres et al., 1982; Tang et al., 2004). For PSR23 and HC-10, the C18 FAs are primarily oleic (18:1) and linoleic (18:2), while all their MCFAs (i.e., C8:0–C16:0) are saturated. The C18 content of seed decreased with decreasing latitude and this was usually concomitant with increased C10:0 content (Table 6). Therefore, the higher seasonal growth temperatures in IL

Table 6
Fatty acid profiles for the direct-planted genotypes by location in 2007 and 2008.

Genotype	Location	2007						2008					
		C8:0	C10:0	C12:0	C14:0	C16:0	C18[‡]	C8:0	C10:0	C12:0	C14:0	C16:0	C18
PSR23	IL	1.1 a[†]	82 a	2.7 a	3.5 a	3.6 b	6.7 c	0.9 ab	84 a	2.3 a	2.3 b	3.2 b	7.3 b
	IA	0.8 b	78 b	2.8 a	4.3 a	4.6 a	9.4 b	1.2 a	80 b	2.6 a	3.6 a	4.2 a	8.5 ab
	MN	0.7 c	77 b	2.6 a	3.2 a	4.2 ab	11.9 a	0.7 b	81 ab	2.5 a	2.3 b	3.6 ab	9.6 a
	ND	0.6 d	77 b	2.8 a	3.3 a	4.2 ab	12.6 a	0.7 b	81 ab	2.4 a	2.5 ab	3.9 ab	9.6 a
	P-value	*<0.0001*	*.001*	*0.79*	*0.34*	*0.05*	*<0.0001*	*0.04*	*0.13*	*0.29*	*0.09*	*0.07*	*0.03*
HC-10	IL	1.0 a	84 a	2.5 a	2.6 a	3.9 ab	6.6 c	0.8 a	84 a	2.4 a	2.3 ab	3.2 a	7.3 b
	IA	0.8 a	81 ab	2.5 a	2.8 a	3.3 b	9.4 b	0.9 a	81 c	3.1 a	2.5 a	3.5 a	8.2 ab
	MN	0.7 a	78 ab	2.4 a	2.6 a	4.0 ab	12.2 a	0.6 a	82 bc	2.3 a	2.0 b	3.5 a	9.5 a
	ND	2.5 a	75 b	2.8 a	3.8 a	4.2 a	11.9 a	1.2 a	83 ab	2.4 a	2.2 b	3.5 a	7.1 b
	P-value	*0.51*	*0.06*	*0.38*	*0.56*	*0.15*	*0.0001*	*0.57*	*0.02*	*0.35*	*0.01*	*0.64*	*0.04*

[†] Values are means, $n = 4$. For each genotype, values within each column followed by the same letter are not significantly different.
[‡] The C18 fraction includes C18:1, C18:2, and C18:3.

Table 7
Fatty acid profiles for the transplanted genotypes by location in 2007 and 2008.

Genotype	Location	2007						2008					
		C8:0	C10:0	C12:0	C14:0	C16:0	C18[§]	C8:0	C10:0	C12:0	C14:0	C16:0	C18
C. wrightii	IL	0.8 a[†]	25 a	63 a	5.2 b	1.4 b	4.5 c	0.5 a	23 c	64 a	5.0 a	1.6 a	5.0 a
	IA	0.5 c	22 a	64 a	6.1 a	1.8 a	5.8 b	0.9 a	24 bc	64 a	5.0 a	1.6 a	4.9 a
	MN	0.7 b	24 a	60 b	6.2 a	2.0 a	7.5 a	0.9 a	27 ab	61 b	6.3 a	2.2 a	8.2 a
	ND	0.7 b	25 a	60 b	5.6ab	1.9 a	6.9 a	1.0 a	29 a	59 b	4.4 a	1.6 a	5.3 a
	P-value	*0.001*	*0.13*	*0.004*	*0.02*	*0.0003*	*0.0002*	*0.50*	*0.004*	*0.11*	*0.41*	*0.23*	*0.20*
C. lutea	IL	–[‡]	–	–	–	–	–	1.6 a	30 a	44 a	9.7 b	2.8 b	12 c
	IA	1.1 a	33 a	35 a	11 a	3.8 a	18 a	1.7 a	29 a	41 ab	10 ab	3.4 a	14 b
	MN	1.3 a	27 a	38 a	12 a	3.6 a	16 a	1.3 a	29 a	38 b	11 a	3.4 a	17 a
	ND	–	–	–	–	–	–	1.3 a	33 a	37 b	10 ab	3.7 a	15 ab
	P-value	*0.18*	*0.38*	*0.55*	*0.24*	*0.51*	*0.22*	*0.21*	*0.64*	*0.06*	*0.16*	*0.001*	*0.0008*
VS6	IL	28 a	44 a	5.9 c	11 b	5.8 c	5.3 d	30 a	42 a	6.7 a	11 a	5.9 a	5.2 c
	IA	25 b	41 ab	6.6 ab	14 a	7.2 b	6.9 c	29 a	41 a	6.2 a	11 a	6.8 a	5.9 bc
	MN	22 c	40 ab	6.7 a	13 a	8.1 ab	9.4 b	30 a	39 a	6.5 a	10 a	6.6 a	7.5 ab
	ND	21 c	39 b	6.2 b	12 b	8.5 a	13 a	26 a	39 a	6.8 a	11 a	7.9 a	8.6 a
	P-value	*<0.0001*	*0.15*	*0.001*	*0.002*	*0.002*	*<0.001*	*0.73*	*0.16*	*0.91*	*0.84*	*0.31*	*0.01*

[†] Values are means, $n = 4$. For each genotype, values within each column followed by the same letter are not significantly different.
[‡] *Cuphea lutea* was not grown in IL or ND during 2007.
[§] The C18 fraction includes C18:1, C18:2, and C18:3.

and IA are probably responsible for the decrease in C18 and increase in C10:0.

The same type of relationship occurred between the predominant MCFAs for the three transplanted genotypes and their C18 content (Table 7). For instance, *C. wrightii* in both years, and *C. lutea* in 2008, showed distinctive increases in lauric acid (C12:0) with decreased C18 content as latitude of field site decreased (Table 7). In 2008, *C. wrightii* showed a significant decline in C10:0 content as C12:0 increased, while *C. lutea*, which is also a lauric-rich cuphea species, did not show this relationship (Table 7). These results agree with those of Thompson et al. (1990) who showed a strong inverse linear relationship between C10:0 and C12:0 contents for the lauric acid-rich *C. wrightii*, but not *C. lutea*. In our study, the range of C12:0 content for *C. wrightii* and *C. lutea* is similar to that reported by Phippen et al. (2006) who measured FA profiles for several accessions of these two species.

VS-6 grown at IL and IA generally showed greater C10:0 content and lower C18 than at MN and ND although differences in C10 during 2008 were not significant (Table 7). In 2007 but not 2008, C8:0 content increased with decreasing latitude of field sites. The C8:0 content ranged from 21 to 30%, while that of C10:0 ranged from 39 to 44% (Table 7), which for most location-yrs was greater than previously reported for VS-6 (Tagliani et al., 1995).

4. Conclusion

In general, *C. wrightii*, *C. lutea*, and VS-6 adapted better to climate and soil conditions found across the Midwest Corn Belt region than PSR23 and HC-10, with the exception of the IA site in 2008 where none of the genotypes fared well because of extremely wet conditions. The relatively high seed and seed oil yield potential of *C. wrightii* and *C. lutea* combined with their high C12:0 content make them good candidates for domestication. Also, because of *C. lutea*'s distribution of C10:0, C12:0, and C14:0 it may lend itself well as a feedstock for making aircraft fuel and other industrial applications. However, developing genotypes with better seed retention will be the biggest obstacle to overcome before these species can be produced on an agronomic scale. If domesticated, these genotypes could serve as a prime source of lauric acid and may be well suited to production over a large geographical area because of their wide range of adaptability. Because of its excellent adaptability and preferable fatty acid profile, *C. lutea* is currently being crossed with the larger, higher yielding PSR23 line (Phippen, 2009).

For the two semi-domesticated genotypes, plant growth and yield correlated best to growing season temperature, which confirms previous work (Forcella et al., 2005; Gesch and Forcella, 2007). However, even though temperature is an important determinant of yield for these genotypes, it is also suggested that pollinator abundance and health related to production location may also play a vital role and clearly deserves further study.

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